THE SKULL OF *DELTACEPHALUS WHITEI*, A LYDEKKERINID TEMNOSPONDYL AMPHIBIAN FROM THE LOWER TRIASSIC OF MADAGASCAR

by R. H. HEWISON

ABSTRACT. The holotype and only skull of *Deltacephalus whitei* from the Lower Triassic of Madagascar, is redescribed and reconstructed. *D. whitei* shares several morphological features with *Lydekkerina huxleyi* and *Limnoiketes paludinatans* and is argued to be a member of the family Lydekkerinidae. Derived characters distinguishing the Lydekkerinidae from other rhinesuchoid temnospondyls are given, and the genus *Deltacephalus* is diagnosed within the family. The Early Triassic littoral temnospondyl fauna from north-west Madagascar is reviewed and compared with contemporaneous temnospondyl faunas from the *Lystrosaurus* Zone of South Africa and the Sticky Keep Formation of Spitsbergen. The Rhytidosteidae and Capitosauridae are represented in all three faunas, whilst the Madagascan fauna is intermediate in sharing lydekkerinids with the South African fauna and trematosaurids with the Spitsbergen fauna.

DELTACEPHALUS whitei Swinton, 1956 is known only from the holotype, BMNH R6695, a small ironstone concretion enclosing natural moulds of a single skull. Swinton (1956) described it as a new genus of rhinesuchoid temnospondyl which he named *Deltacephalus whitei*. He believed *Deltacephalus* to be related to the poorly known lydekkerinid temnospondyl *Broomulus dutoiti* from the *Lystrosaurus* Zone of South Africa, and so assigned it to the Lydekkerinidae.

Deltacephalus is one of several temnospondyl genera described from the Lower Triassic Middle Sakamena Group of north-west Madagascar. Our knowledge of these temnospondyls derives mainly from the work of Lehman (1955, 1961, 1963, 1966, 1979) who described most forms and discussed their relationships. *Deltacephalus* was not, however, included in these studies and is considered by most recent authors to be unclassifiable below Stereospondyli *incertae sedis* (e.g. Cosgriff 1974, p. 43; Milner 1990, p. 348).

As part of a revision of the Lydekkerinidae, new casts were made at the Natural History Museum, London, and these, together with study of the original moulds and earlier plaster casts have permitted a more extensive description of the specimen, including many new details of the skull roof, palate and occiput.

Institutional abbreviations used in this work are as follows: BMNH, The Natural History Museum, London, UK; BPI, Bernard Price Institute, Johannesburg, South Africa; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; UMZC, University Museum of Zoology, Cambridge University, UK.

MATERIAL AND METHODS

The concretion bearing the skull is broken into three closely fitting pieces, two larger fragments bearing impressions of the skull roof and palate respectively, while the smaller third piece bears an impression of the occipital surface. The impression of the dorsal surface of the skull is well preserved, those of the palate and the occiput less so. The skull lacks the extreme anterior region of the snout and a few small areas along its posterior edge, whilst much of the palate anterior to the interpterygoid vacuities is missing. The occipital surfaces of both cheek regions are obscure and the skull has suffered some compression over the snout region and also on its right side, particularly behind the orbit.

In 1993 new peels of the specimen were made at the Natural History Museum, London, using 'Wacker' cold cure silicone rubber, to complement older plaster and coloured 'Welvic' casts.
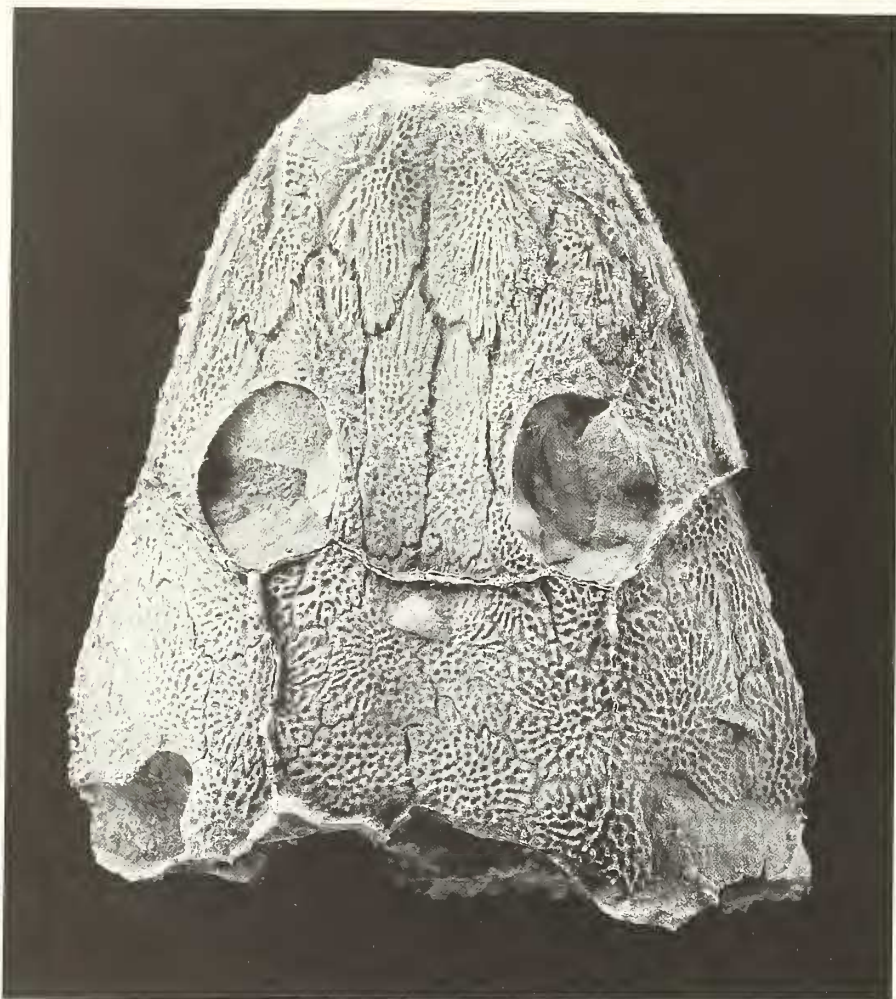
TEXT-FIG. 1. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Silicone rubber peel of dorsal aspect of holotype skull BMNH R6695; ×2.

Photographs of these new peels, coated with graphite to highlight detail, illustrate this work (Text-figs 1, 4). Under the binocular microscope, detail was easier to see on the 'Welvic' casts and the following description and Text-figures 2–3 and 5–8 are based on study of these and the original specimen.
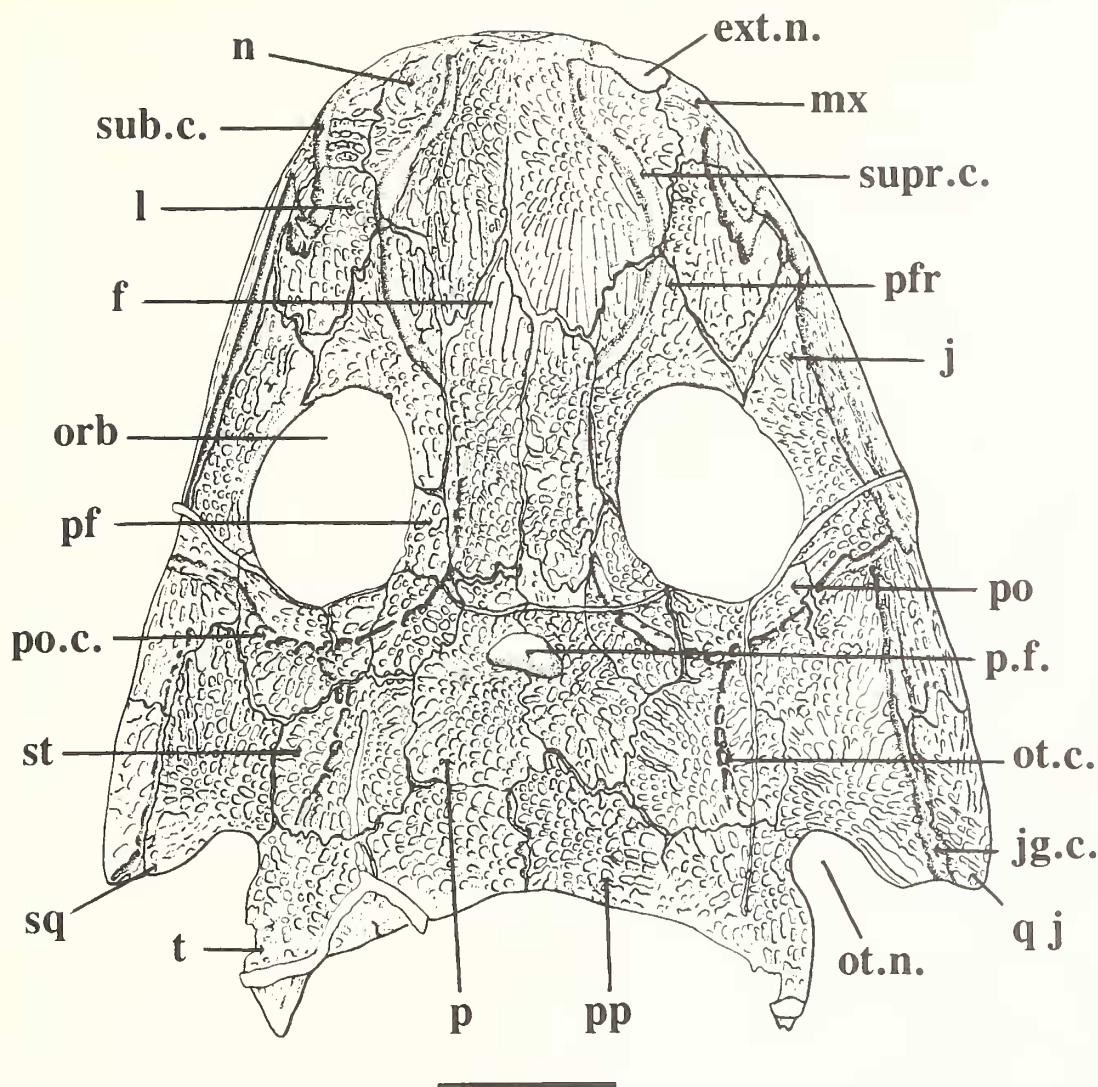
SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758
Order TEMNOSPONDYLI von Zittel, 1890
Family LYDEKKERINIDAE Watson, 1919

Genus DELTACEPHALUS Swinton, 1956

Type species. *Deltacephalus whitei* Swinton, 1956.

Diagnosis. As for the only species.

TEXT-FIG. 2. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, dorsal surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

Deltacephalus whitei Swinton, 1956

Text-figures 1–8

Holotype and only specimen. BMNH R6695, a small ironstone concretion enclosing a complete skull represented by natural moulds.

Locality and horizon. Ambarakaraka, 8 km north of Anaborano, north-west Madagascar; Middle Sakamena Formation, Induan, Lower Triassic.

Diagnosis. Distinguished from other lydekkerinids by the following combination of characters: skull parabolic with broadly rounded snout; lateral margins slightly sinuous; quadratojugal corners

anterior to level of middle of posterior skull table margin; tabular horns long and curved; parietal foramen oval; prominent lateral-line system with deep lyrae; cultriform process striated ventrally with weak keel; parasphenoid corpus ridged, bearing poorly developed stapedial lappets; palatal ramus with slight pterygoid flange; interpterygoid vacuities and occipital openings relatively large; opisthotic not exposed in paroccipital bar.

Description

Skull roof (Text-figs 1–3, 7). This skull, like those of all lydekkerinids, is small, moderately flattened and as short as it is broad. As preserved, it has a median length of 48 mm and a maximum width of 49 mm (Text-fig. 2). It has a rounded snout and its slightly sinuous lateral borders give it a broadly parabolic outline. The posterolateral corners of the quadratojugals lie slightly ahead of the level of the midpoint of the posterior margin of the skull table. The tabular horns are relatively long and curved, and are more fully developed than Swinton's figure suggests. The large orbits have a central position on the skull roof, resulting in the short preorbital region that characterizes all lydekkerinids. In profile, the skull appears depressed, particularly in the facial region, exaggerated somewhat by the dorso-ventral compression of the snout (Text-fig. 3). The central
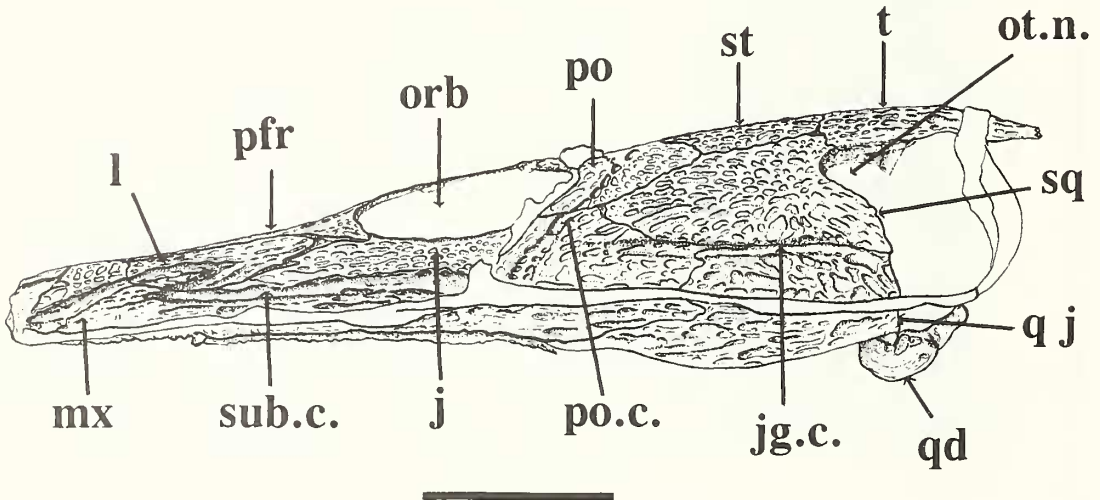
TEXT-FIG. 3. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, left lateral view, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

hollowing seen on the roof of *Lydekkerina* is paralleled here, and the cheek regions similarly curve gently ventrolaterally from the skull table.

The impression of the dorsal surface of the skull is well preserved and most of the sutures are clearly visible. The sensory openings are relatively very large (Text-figs 1–3). Little can be seen of the external nares because of the loss of the anterior tip of the snout, but there appear to be traces of the posterior region of the right naris. There is no evidence to support Swinton's reconstruction of the nares as narrow and transversely situated. The large, oval orbits have less elevated margins than in *Lydekkerina* and the large parietal foramen, although distorted, appears to have been broader than long, and of an oval rather than circular shape. Its present kidney-shaped outline is probably an artefact of preservation. The well developed U-shaped otic embayments, which are incised quite deeply into the squamosals and open posteriorly, are similar to those of *Lydekkerina* and *Limnoiketes.*

As a result of local compression, the right roofing bones now appear as slightly larger than their left counterparts. Both premaxillaries are missing and septomaxillaries cannot be seen. Posterior to the exterior

TEXT-FIG. 4. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Silicone rubber peel of palatal aspect of holotype skull BMNH R6695; ×2.

naris, the nasal and maxillary meet to exclude the lacrimal from the narial border. The lacrimals, far from having the very unusual jagged outlines figured by Swinton, are relatively small elongated bones of orthodox shape. Swinton incorrectly identified part of the suborbital sulcus, with its characteristic lacrimal flexure, as the outer border of the lacrimal. As in *Lydekkerina* and *Limnoiketes*, the frontals are separated from the orbits by
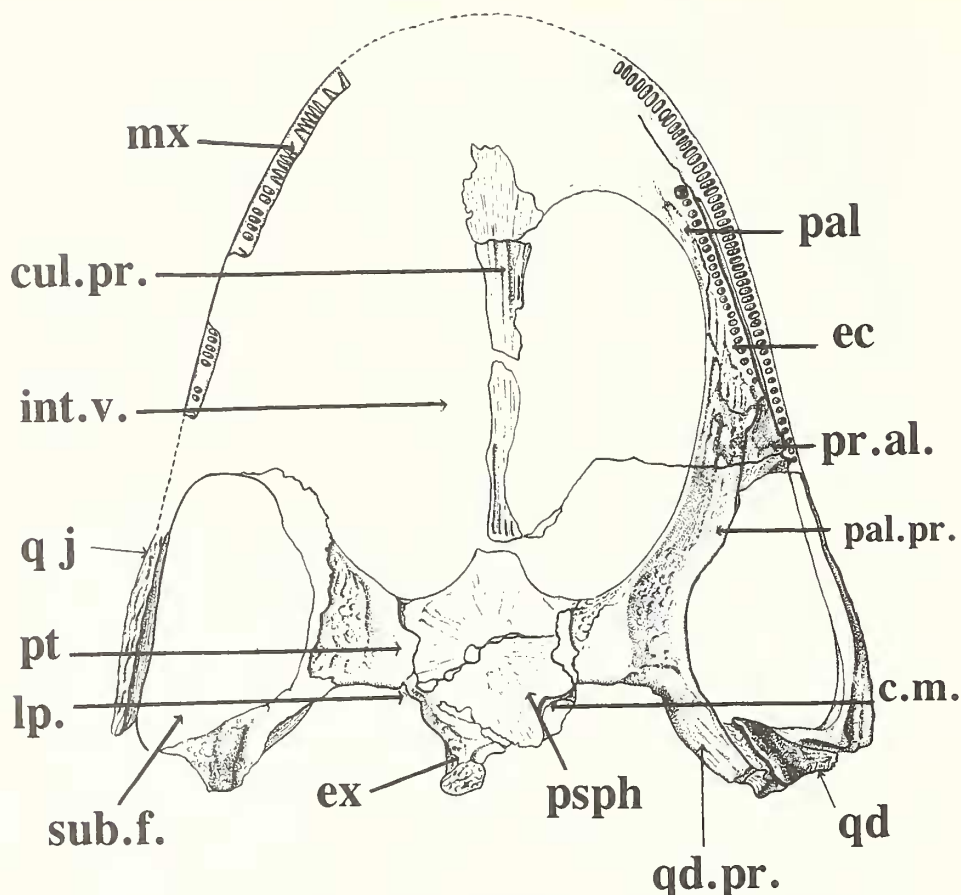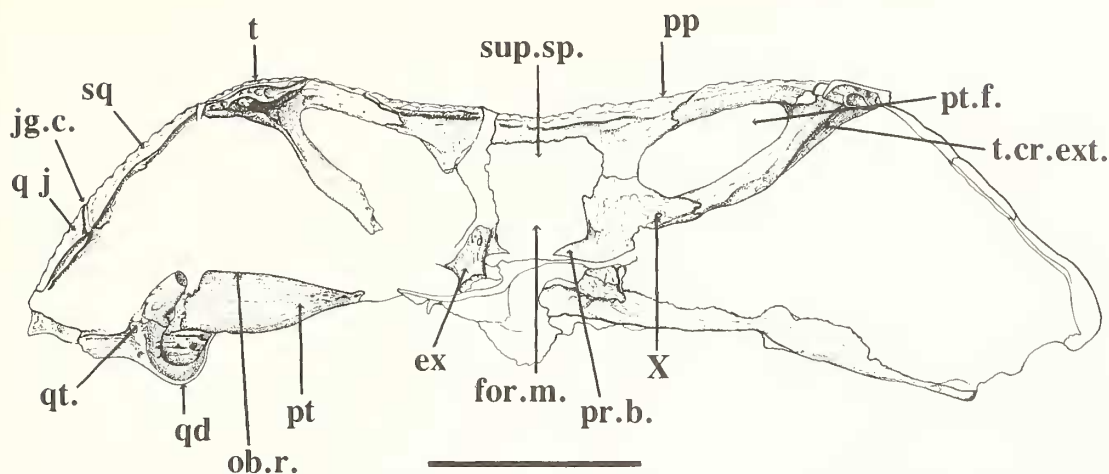
TEXT-FIG. 5. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, palatal surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

the prefrontal–postfrontal contact, and the supratemporals from the otic embayments by the squamosal–tabular contact.

As in other lydekkerinids, the dermal ornament of the roofing bones consists of a network of ridges which separate either rounded depressions or more elongated grooves. The ornament is best seen on the casts (Text-fig. 1), where, in the unworn areas, the ridges are smoothly rounded and form slight conules where they meet each other as in *Lydekkerina* and *Limnoiketes*. The depressions vary considerably in size and outline, and tend to cover the more central areas of the bones. Grooving is generally restricted to the peripheral areas, and ornamentation often appears to radiate away from the ossification centre of the bone. The presence of a preorbital zone of intensive growth is indicated by the pronounced grooving of the ornament over the posterior third of the nasals and the neighbouring portions of the frontals and prefrontals. Less pronounced postorbital grooving occurs over the posterior region of the jugal, and over the neighbouring margins of the squamosal and quadratojugal.

The lateral-line system is more extensive than Swinton indicated and, as is normal for lydekkerinids, the sulci appear partly as grooves and partly as rows of depressions (Text-figs 1–3). The grooves are deep and wide. Several sulci pass over, or close to, the ossification centres of bones. The supraorbital sulcus forms a typical lyra over the facial region where it is developed as a deep and wide groove, but its interorbital section consists of a series of separate shallow depressions. The suborbital sulcus, clearly visible on the left side of the skull, forms a deep and wide groove crossing the jugal and maxillary, and having the usual lacrimal flexure over the

TEXT-FIG. 6. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, occipital surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

maxillary and lacrimal. The jugal, postorbital and otic sulci were neither described nor figured by Swinton, but are visible on the new casts. The otic sulcus is an extensive series of depressions which leaves the postorbital sulcus and curves across the supratemporal.

Palate (Text-figs 4–5, 8A). The impression of the palatal surface is less well preserved than that of the cranial roof. Apart from the very poorly preserved region anterior to the interpterygoid vacuities, most of the structure of the palate can be described from one side or the other. The palate is slightly distorted, however, and the anterior region of the cultriform process has been crushed against the skull roof, while the left quadrate is partly detached from the quadrate ramus of the pterygoid.

The palate is characterized by the very large interpterygoid vacuities and subtemporal fossae, separated and bordered by relatively slender struts of bone (Text-figs 4–5). The interpterygoid vacuities extend over half the length of the palate and are not so narrow and anteriorly pointed as depicted by Swinton. Nearly all of the outline of the left vacuity is visible and it is slightly broader anteriorly than posteriorly. The subtemporal fossae extend anteriorly well ahead of the posterior borders of the interpterygoid vacuities, and the well preserved left fossa has a length almost one-third of that of the skull. It lacks the simple hemispherical outline figured by Swinton, but is rather 'pear-shaped' being broadly rounded posteriorly, and narrower and more elongated anteriorly (Text-fig. 5).

The parasphenoid has a well-developed corpus with moderately long sutural contacts with the pterygoids, and with a series of fine ridges radiating away from the centre of the palatal surface. On its left side, towards its posterolateral corner, there appears to be a crescentic, ridge-like crista muscularis, which overhangs slightly a shallow depression which appears to represent a 'pocket' for the insertion of a rectus capitis muscle (Text-fig. 5). Both crista and pocket are less well developed than in *Lydekkerina* and *Limnoiketes*, but as in these forms, the crista faces posterolaterally and lies well ahead of the condylar region, towards the posterior end of the parasphenoid–pterygoid suture. The bone surface on the corresponding regions of the right side of the corpus has been abraded and shows no trace of either crista or pocket.

On both sides of the specimen, the posterior margin of the parasphenoid corpus gives the impression of having been produced backwards to form a stapedial lappet, but this is far less developed than in the other lydekkerinids. The sutures between the parasphenoid and the exoccipitals cannot be clearly seen.

The cultriform process, though broken, slightly displaced, and partly obscured by matrix, appears to have been a long and relatively broad blade. It terminates anterior to the interpterygoid vacuities as an expanded, broad, V-shaped wedge lying between the vomers. It bears a series of ventral ridges, generally parallel to its long axis, and there is a suggestion of a slight, narrow, median keel.

The left pterygoid is well exposed on the casts and closely resembles those of *Lydekkerina* and *Limnoiketes* in possessing ornament over the lateral portions of its corpus, the palatal ramus and the base of the quadrate ramus (Text-fig. 5). The proportions of the pterygoid differ considerably from those figured by Swinton. The
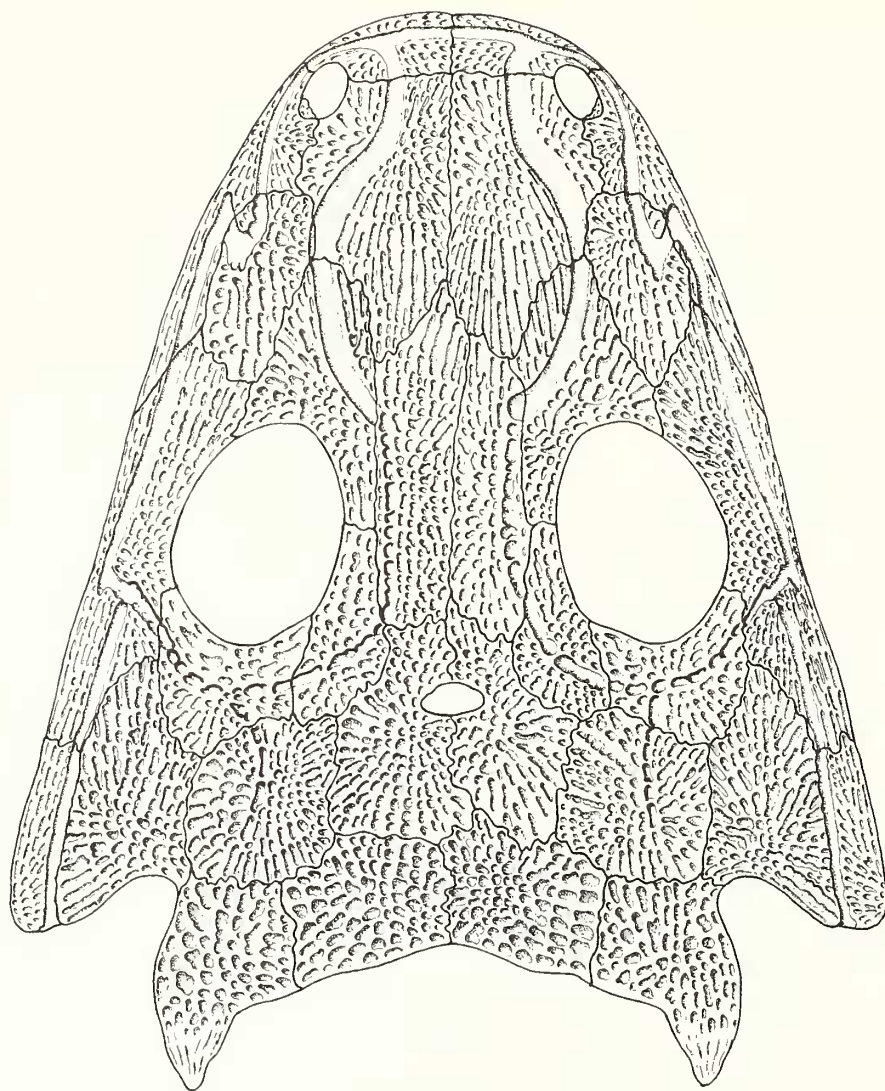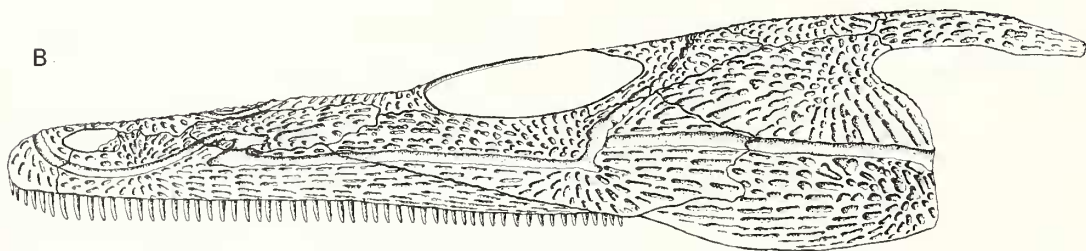
TEXT-FIG. 7. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Reconstruction of the skull in A, dorsal view; B, left lateral view.

corpus is broad and has a moderately long common suture with the parasphenoid, although details of this are not visible. Its ventral surface has a raised medial area almost devoid of ornament and a more depressed lateral ornamented area.

The long and moderately broad palatal ramus has a shallow pterygoid flange protruding into the subtemporal fossa and it tapers anteriorly to suture with a probable processus alaris of the jugal, and anterior to this, with an ectopterygoid. The ramus appears to extend slightly more than half-way around the border of the interpterygoid vacuity, but it is not clear where or not it sutured with the palatine. The ramus is hollowed out for most of its length, the hollow being bordered by a ridge mesially, and by a distinct upturned flange laterally which bounds the subtemporal fossa. The ornament on the anterior ramus is particularly striking, forming a series of elongate ridges and grooves.

The quadrate ramus is much shorter and more slender than the palatine ramus but is also ornamented proximally with depressions and ridges, although in a less pronounced manner. The quadrate, hitherto undescribed, is visible on the left side. It is a stout ossification, bearing a well-defined convex condylar keel medially but becoming lower and narrower laterally where it is firmly clasped anteriorly and posteriorly by mesially directed paraquadrate laminae from the quadratojugal (Text-figs 4–5). A ridged swelling at the base of the anterior lamina probably buttressed a smaller lateral condylar keel although this cannot be seen because the lateral end of the quadrate is missing.

A processus alaris from the jugal appears to have been exposed by disturbance immediately anterior to the left subtemporal fossa (Text-figs 4–5). It is a roughly triangular bone, lacking palatal teeth. Anterior to it lies a narrow ectopterygoid which bears the posterior portion of a palatal tooth row laterally, except at its posterior end. None of the ectopterygoid sutures are visible clearly and it is uncertain whether the ectopterygoid reached the margin of the interpterygoid vacuity or was excluded by a backward extension of the palatine. The palatine bears along its entire lateral border an anterior continuation of the tooth-row seen on the ectopterygoid. This row comprises 20 teeth and two pits, and terminates in a larger, more rounded, fang on a level just anterior to the front end of the interpterygoid vacuities. This fang is probably one of the pair of palatine fangs normally situated just posterior to the choana. The following palatal tooth-row is similar to that of other lydekkerinids in lacking ectopterygoid fangs.

Some hitherto unreported details of the maxillary teeth can be made out. The palatal portion of the left maxillary forms a slender strip of bone extending from the anterior end of the subtemporal fossa along the whole of the preserved lateral border of the skull (Text-fig. 5). It bears a long, continuous row of closely set, small teeth which are relatively long and slender with slightly recurved tips. About 39 teeth and 11 pits have been preserved, suggesting space for 50 teeth in each maxillary. The teeth enlarge over the anterior half of the tooth row, reaching a maximum length of 2 mm. In the right maxillary, two toothed portions survive, the more anterior with 19 teeth and the posterior fragment with eight. The maxillary teeth are slightly larger than the palatal teeth.

Occiput (Text-figs 6, 8B). The impression of the occipital surface is only partly preserved, but is easier to interpret from the specimen than from the casts because of the contrast between its black colour and the paler surrounding matrix. Although the occiput has been crushed slightly on its right side, with parts having been displaced, certain aspects of its structure can be ascertained. Several new features can be added to Swinton's account, and the occipital surface is figured here for the first time.

The occipital surface, like the palate, is characterized by having large openings separated and bounded by relatively slender struts of bone (Text-figs 6, 8B). The posttemporal fossa is complete on the right side of the impression and is seen to be roughly egg-shaped with its narrower end directed dorsolaterally. The essentially triangular foramen magnum has a wide base that is floored partially by a pair of basal processes from the exoccipitals and it narrows dorsally before opening into a wide supraoccipital space. Also visible is the broken-off remnant of the right exoccipital process which once supported the cartilaginous supraoccipital.

On the right side, the occipital flanges of the postparietal and tabular are clearly visible, as are the rising flanges of the exoccipital which suture with them. The complete, right paroccipital bar shows that, as in *Limnoiketes*, the opisthotic is not incorporated, and that the tabular extends down to the exoccipital, forming the major part of the ventral border of the posttemporal fossa. The lateral limits of the exoccipital on the bar are indicated by a meandering suture on the impression, which crosses the bar a quarter of the way up its length from its base. The corresponding portion of the left paroccipital bar is missing.

The preserved right occipital process of the tabular is greatly expanded and thickened proximally to provide strong support for the tabular, whilst the tabular horn was also supported ventrally by a strongly developed crista tabularis externa which, as in *Lydekkerina* and *Limnoiketes*, runs along the posterolateral border of the process and onto the underside of the tabular horn.
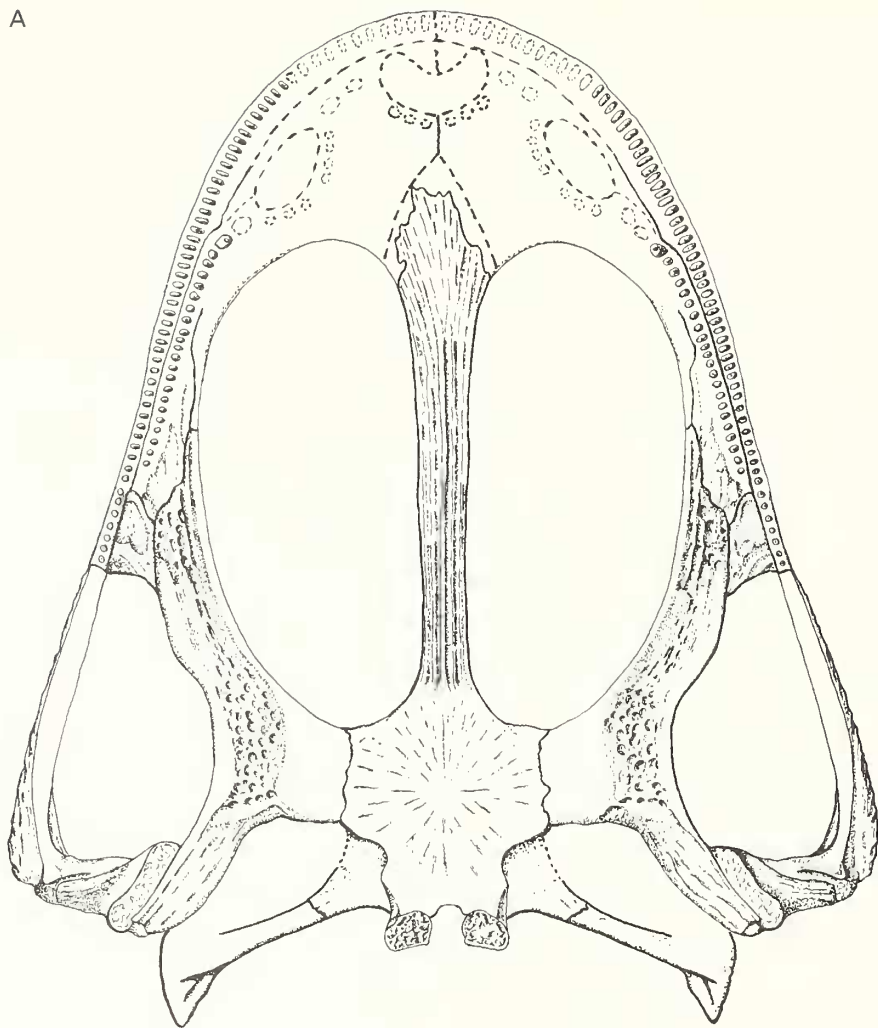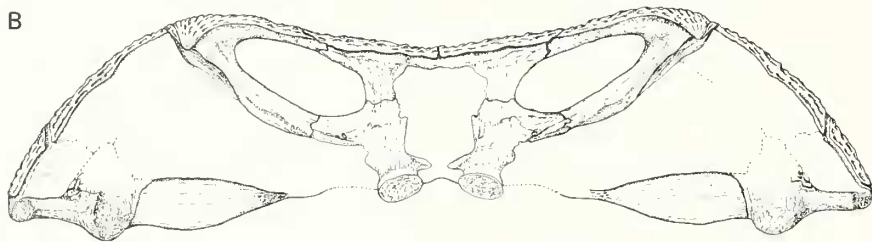
TEXT-FIG. 8. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Reconstruction of the skull in A, palatal view; B, occipital view.

Each exoccipital consists of a relatively wide vertical column, bordering the foramen magnum, from which arise the usual four processes. Just below the origin of the processus basalis, each exoccipital gives rise to a condyle. The left condyle is exposed on the casts but is directed slightly ventrally, whilst the right condylar surface can also be seen in occipital aspect. The condyles are widely separated, as in all lydekkerinids. Each condyle terminates in an expanded, oval, unfinished articulatory surface, wider than deep and borne upon a short columnar stalk. The condyles probably projected slightly behind the plane of the occiput, with their articulatory surfaces facing posteromedially and slightly ventrally. Above the base of the left condyle is a small foramen, perhaps for a nutritive vessel, while a further foramen (X, Text-fig. 6), possibly for the vagal nerve, opens on the right parotic process just above a slight ridge running outwards along the process.

An oblique ridge appears to be present on the left quadrate ramus of the pterygoid, and a roughened, slightly nodular quadrate tubercle is visible just lateral to the upper end of the large inner condylar keel (Text-fig. 6). Both features are present in the other lydekkerinids.

Reconstruction (Text-figs 7–8). Much of the reconstruction of the skull roof and palate of *Deltacephalus* is based on the least distorted left side of the holotype skull, but for the occiput (Text-fig. 8B) the better preserved right side has been used. As reconstructed, the skull is narrower and deeper than it appears in the casts. The missing front end of the snout has been reconstructed on the basis of *Lydekkerina*, and a septomaxillary and an ethmoidal sulcus have been added. The ornamentation, although simplified, is based on the best preserved areas.

Systematic position

This redescription of the type skull of *Deltacephalus* supports Swinton's original conclusion that this genus belongs to the Lydekkerinidae. This family was established by Watson (1919) exclusively for *Lydekkerina* (*Bothriceps*) *huxleyi*, a relatively small, short-faced temnospondyl from the Lower Triassic *Lystrosaurus* Zone of South Africa. Subsequently, ten additional species have been referred to the family: *Lydekkerina putterilli* Broom, 1930; *Putterillia platyceps* Broom, 1930; *Broomulus dutoiti* (Broom) Romer, 1947; *Limnoiketes paludinatans* Parrington, 1948; *Lydekkerina kitchingi* Broom, 1950; *Deltacephalus whitei* Swinton, 1956; *Lydekkerina pancheteusis* Tripathi, 1969; *Cryobatrachus kitchiugi* Colbert and Cosgriff, 1974; *Chomatobatrachus halei* Cosgriff, 1974; and *Luzocephalus blomi* Shishkin, 1980.

A revision of the lydekkerinid genera *Lydekkerina* and *Limnoiketes* has recently been completed by the author, involving re-examination of much material of *Lydekkerina huxleyi* including the holotype (BMNH R507) and the skulls described by Broili and Schröder (1937; BSP 1934 VIII 44), by Parrington (1948; UMZC T206 and T238), and by Watson (1951; UMZC T110). Undescribed specimens studied included BMNH R504–R506, R508, R3909, R5482 and R6850 and the mandible BPI 1373. The holotype of *Limnoiketes paludinatans* (UMZC T214) was also studied. It is a conclusion of this reappraisal of the Lydekkerinidae that the content of the family should be restricted to the three determinate genera *Lydekkerina*, *Limnoiketes* and *Deltacephalus*, and so the following comparisons with *Deltacephalus* were made with the above listed material.

Deltacephalus is similar to *Lydekkerina* and *Limnoiketes* in many respects but can nevertheless be diagnosed as a separate genus. The following characters vary between the three genera.

1. Skull shape. All three forms have a skull which is parabolic in outline when seen from above. In *Lydekkerina* the lateral skull margins are gently convex, in *Deltacephalus* they are slightly sinuous, whilst in *Limnoiketes* the margins are more irregular, being convex near the snout and the temporal regions and concave in between. The skulls of both *Lydekkerina* and *Deltacephalus* are relatively depressed in comparison with that of *Limnoiketes* which is not only domed in the region of the parietal foramen but is also unusually deep in the orbital and postorbital regions. The orbits are more laterally directed in *Limnoiketes* than in *Lydekkerina* or *Deltacephalus*.

2. Lateral-line sulci. In *Deltacephalus* the well-developed lateral-line sulci take the form of deep grooves. The system is less prominent in *Lydekkerina* and the lyrae are not wide and deeply excavated but consist of a series of separate depressions. The system is only weakly developed in *Limnoiketes*.

3. Tabular horns. In *Deltacephalus* the tabular horns are stout, curved and backwardly directed. In

Lydekkerina and *Limnoiketes*, they are bluntly rounded and relatively laterally directed. The horns are prominent in *Lydekkerina* but are very reduced in *Limnoiketes*.

4. Quadratojugal extent. In *Deltacephalus* the posterior end of the quadratojugal lies ahead of the midpoint of the posterior edge of the skull table. In *Lydekkerina* and *Limnoiketes* the posterior end of the quadratojugal lies behind the midpoint of the posterior edge of the skull table.

5. Parietal foramen. In *Lydekkerina* and *Limnoiketes* the parietal foramen is circular; in *Deltacephalus* it is oval.

6. Palate shape. In *Deltacephalus* the interpterygoid vacuities and subtemporal fossae are relatively larger than in other lydekkerinids. The interpterygoid vacuities are of elongate oval shape whereas they are shorter and narrowly rounded posteriorly in *Lydekkerina* and shorter and broader posteriorly in *Limnoiketes*.

7. Parasphenoid. In *Deltacephalus* the parasphenoid has a narrow, striated and weakly keeled cultriform process. In *Limnoiketes* the cultriform is also narrow but is not striated or keeled. In *Lydekkerina* it is broader and is denticulate and grooved laterally over its posterior half. The corpus of the parasphenoid is ridged in *Deltacephalus* and bears poorly developed stapedial lappets. Well-developed stapedial lappets, protruding backwards, are present in *Limnoiketes* and pronounced in *Lydekkerina*.

8. Pterygoid. The palatine ramus of the pterygoid of *Deltacephalus* has a shallow pterygoid flange and is intermediate between that of *Limnoiketes* which has a pronounced pterygoid flange and that of *Lydekkerina* which lacks this feature entirely.

9. Occiput. In *Deltacephalus* and *Limnoiketes* the opisthotic is not exposed in the paroccipital bar. In *Lydekkerina* the opisthotic is fully ossified and occupies the central portion of the bar.

The above comparisons are summarized in the diagnosis of *Deltacephalus whitei*.

Deltacephalus *and the Lydekkerinidae*. Lydekkerinidae has always been a difficult family to define, principally because lydekkerinids are small forms with short, broad skulls which display so many 'juvenile' features that they are not easy to distinguish from the juvenile stages of larger temnospondyls. These features include the relatively large size of the sensory, palatal and occipital openings, the central position of the orbits on the skull roof, the proximity of the parietal foramen to the level of the posterior margin of the orbits, and the quadrates being on the same level as the exoccipital condyles.

Lydekkerinids have traditionally been associated with the temnospondyl families Rhinesuchidae and Uranocentrodontidae in the superfamily Rhinesuchoidea and are clearly closely related to them, although the Rhinesuchoidea may be a grade of organization rather than a clade (Milner 1990). Lydekkerinids can be distinguished from rhinesuchids and uranocentrodontids by the following derived characters: presence on the occiput of a distinct squamosal–quadratojugal trough; presence of pronounced dermal ornamentation on the main body and rami of the pterygoid instead of a denticulate surface; presence on the mandible of an extensive and complex postglenoid area in which a long surangular process is separated from a short retroarticular process by a prominent depressor groove; a large hamate process; a prearticular which does not extend past the splenial–postsplenial suture; and coronoid denticles confined to the posterior coronoid.

Some of these characters occur sporadically in other Triassic temnospondyl families such as the Rhytidosteidae, the *Derwentia*-group (Milner 1990), but particularly in the Capitosauridae which has long been recognized as being close systematically to the temnospondyls of the rhinesuchoid grade and which shares with them such features as a buttressed tabular horn, stapedial groove, oblique ridge and quadrate tubercle. In contrast with the Lydekkerinidae, in the Capitosauridae the cristae musculari have lost their crescentic form and are usually confluent, forming one continuous, shallow V-shaped ridge; stapedial lappets are almost always absent; and the frontals enter the orbit margins (Warren and Hutchinson 1988*a*). More significantly, the Capitosauridae never developed the complex postglenoid area of the lydekkerinids.

The small size of the lydekkerinids and the unusual abbreviation of their snout region may also be derived characters for the group. There is indirect evidence, based on the uniformity in size of

specimens of *Lydekkerina*, growth studies of related temnospondyls, and the ontogeny of the temnospondyl skull, to suggest that lydekkerinids are small adult temnospondyls and not the growth stages of larger temnospondyls. The juvenile appearance would not seem to be due to neoteny, as is testified by the presence of a quadrate tubercle and by the high degree of ossification of the neurocranium in UMZC T110, and is more probably the result of progenetic dwarfing accompanied by reduced allometric growth of the snout, as suggested by Milner (1990, 1991).

Deltacephalus is not so completely preserved as either *Lydekkerina* or *Limnoiketes* and, lacking mandibles, does not display so many of the derived characters that serve to define the family. It can be confirmed as a lydekkerinid, however, by the well-developed dermal ornamentation on the pterygoid, and by the shortness of the snout region and the very low preorbital index to which this gives rise (for details see Colbert and Cosgriff 1974; Cosgriff 1974). In the reconstructed skull of *Deltacephalus* this index is 44, which is remarkably close to the index of 43 for the types of both *Lydekkerina huxleyi* and *Limnoiketes paludinatans*. It is well below the indices of similar sized skulls belonging to young growth stages of capitosaurids and benthosuchids, all of which exceed 53. The validity of this preorbital index as a criterion to distinguish lydekkerinids has been criticized (Warren and Black 1985) but has been confirmed to the present author's satisfaction by studies on the growth stages of temnospondyls. These indicate that the adult condition of the snout region (short or long) is already at least partly expressed in the skulls of immature post-metamorphic temnospondyls, just as other adult derived features are (Warren and Hutchinson 1988*b*). *Deltacephalus*, therefore, along with *Lydekkerina* and *Limnoiketes*, can be considered as a genuine small, short-snouted adult lydekkerinid and not merely the growth stage of a longer snouted form.

THE EARLY TRIASSIC TEMNOSPONDYL FAUNA OF MADAGASCAR

Lehman (1979) considered the Early Triassic temnospondyl fauna from the Sakamena Formation of Madagascar to be littoral, composed of marine trematosaurids and freshwater benthosuchids and a rhinesuchoid. The presence of associated ammonites confirmed the marine nature of the deposits and Lehman assumed that the freshwater forms were transported in via rivers, although they showed no traces of fluviatile erosion. The fauna, as identified by Lehman, comprised one rhinesuchoid (*Mahavisaurus dentatus*), two benthosuchids (*Benthosuchus madagascarensis*, *Wetlugasaurus milloti*) and five to seven trematosaurids (*Wantzosaurus elongatus*, *Lyrosaurus australis*, *Trematosaurus madagascarensis*, *Ifasaurus elongatus*, *Tertremoides ambilobensis*, together with *Aphaneramma* sp. and *Tertrema* sp.).

Lehman briefly compared this fauna with others from the Early Triassic and concluded that it most closely resembled that of the Sticky Keep Formation of Spitsbergen. This was also a littoral assemblage, containing both ammonites and a mixture of presumed marine and freshwater temnospondyls. The fauna as known then comprised one possible capitosaurid (*Sassenisaurus spitsbergensis*), one possible brachyopid (*Boreosaurus thorslundi*), two rhytidosteids (*Peltostega erici* and *P. wimani*) and four trematosaurids (*Aphaneramma rostratum*, *Lyrocephaliscus* (= *Lyrocephalus*) *euri*, *Platystega depressa* and *Tertrema acuta*). Lehman believed that the Madagascan trematosaurids *Wantzosaurus* and *Lyrosaurus* resembled the Spitsbergen trematosaurids *Aphaneramma* and *Lyrocephaliscus* respectively, but in other respects, the faunas seemed quite distinct.

Many of Lehman's taxonomic conclusions have, however, been superseded by later work. *Benthosuchus madagascarensis*, described by Lehman (1961, 1966), was reinterpreted by Shishkin and Lozovskiy (1979) and Warren and Hutchinson (1988*a*) as a capitosaurid. The latter authors redescribed the holotype as *Parotosuchus madagascarensis* and argued that all Madagascan material assigned by Lehman to *Benthosuchus* and *Wetlugasaurus* should be referred here, and that this was the only capitosaurid in the fauna. However, Welles and Cosgriff (1965) had suggested that the Madagascan *Wetlugasaurus* was more closely allied to the rhinesuchids than to the capitosaurids. *Mahavisaurus dentatus* and *Lyrosaurus australis* were described by Lehman as a rhinesuchoid and a trematosaurid respectively (Lehman 1966, 1979), but have been perceived subsequently by many authors to be immediately related members of the family Rhytidosteidae (Howie 1972; Cosgriff and

Zawiskie 1979; Shishkin 1980; Warren and Black 1985; Milner 1990, 1991). Cosgriff and Zawiskie (1979) concluded that they were two species of the genus *Mahavisaurus*, a view subsequently endorsed by Warren and Black (1985) and Milner (1990, 1991). Of the many trematosaurids described by Lehman, subsequent workers have accepted only *Wantzosaurus elongatus*, *Trematosaurus madagascarensis* and *Tertremoides ambilobensis* as valid taxa, while the other taxa are perceived as indeterminate (Cosgriff 1984; Welles 1993).

The taxonomy of the Spitsbergen temnospondyls has remained much more stable, the only revision being that of Shishkin and Vavilov (1985) who argued that the poor material of *Boreosaurus thorslundi* is probably rhytidosteid rather than brachyopid.

Thus, with the revision here of *Deltacephalus*, the Early Triassic temnospondyl fauna from Madagascar now comprises the following taxa:

Capitosauridae: *Parotosuchus madagascarensis*
Lydekkerinidae: *Deltacephalus whitei*
Rhytidosteidae: *Mahavisaurus dentatus*
                    Mahavisaurus australis
Trematosauridae: *Wantzosaurus elongatus*
                    Trematosaurus madagascarensis
                    Tertremoides ambilobensis

The Early Triassic fauna of Spitsbergen is:

Capitosauridae: *Sassenisaurus spitsbergensis*
Rhytidosteidae: *Peltostega erici*
                    Peltostega wimani
                    Boreosaurus thorslundi
Trematosauridae: *Aphaneramma rostratum*
                    Lyrocephaliscus euri
                    Platystega depressa
                    Tertrema acuta

These taxonomic revisions serve to enhance the limited resemblance that Lehman had noted between these faunas, with both possessing presumed marine trematosaurids and presumed freshwater rhytidosteids and capitosaurids.

The only other Early Triassic temnospondyl assemblage which contains undoubted lydekkerinids is that of the *Lystrosaurus* Zone of South Africa. Lehman (1961, 1979) found little in common between this fauna and that from the Sakamena Formation, but the taxonomic changes noted above suggest some similarity.

The *Lystrosaurus* Zone temnospondyl fauna is currently perceived as:

Rhinesuchidae: *Uranocentrodon senekalensis*
Capitosauridae: *Kestrosaurus dreyeri*
Lydekkerinidae: *Lydekkerina huxleyi*
                    Limnoiketes paludinatans
Rhytidosteidae: *Rhytidosteus capensis*
                    Pneumatostega potamia
Micropholidae: *Micropholis stowi*
Brachyopidae: unnamed fragments.

In both faunas, therefore, lydekkerinids, rhytidosteids and a capitosaurid are present. The South African fauna is not a littoral one, however, but a continental one in which the temnospondyls inhabited broad low-gradient flood-plains, transient shallow pools and lakes, and wide shallow impersistent rivers (Kitching 1978). The fauna is dominated by reptiles, and some of the amphibians, such as *Micropholis* (often associated with the procolophonid *Procolophon*) and *Limnoiketes* (a single exotic specimen), were probably largely terrestrial.

The *Lystrosaurus* Zone temnospondyls are more locally abundant than those in Madagascar,

perhaps because the majority of them were preserved in the beds of the ponds and lakes in which they lived. Many are well preserved with articulated postcranial skeletons (e.g. *Lydekkerina*, *Micropholis*, *Uranocentrodon*). The presumed continental elements in the Madagascan fauna are less well preserved with postcranial material less in evidence. The presence of well preserved skulls, however, suggests that only restricted post-mortem transport occurred and hence that they may have lived in coastal lagoons or deltaic rivers or streams. In the Sticky Keep fauna, the presumed continental/freshwater forms are relatively scarce and more fragmentary than their Sakamena Formation counterparts which might indicate transport from a greater distance either from further inland or further out to sea.

Recent work on the $^{87}Sr/^{86}Sr$ ratio in the bones of Spitsbergen temnospondyls and in coprolites assigned to them indicates that they did not live exclusively in marine or freshwater conditions but possessed an intermediate ratio suggestive either of a littoral life-style or anadromy (Lindemann 1991). The presence of wrinkle-marks and channel-fillings in the temnospondyl-producing beds indicate shallow-water conditions, although sedimentological studies combined with the *in situ* embedding of the coprolites in the marine deposits suggest that part of the Sticky Keep Beds was laid down in open marine environments (Mork *et al.* 1982). It thus appears that at least some of the temnospondyls at Sticky Keep spent parts of their lives in the sea. It is possible to hypothesize that the more abundant and better preserved trematosaurids were truly marine forms as adults, though possibly anadromous, while the rhytidosteids and capitosaurids were littoral or continental and present only as exotic elements in the fauna.

The littoral fauna from the Sakamena Formation appears to occupy an intermediate position between the continental *Lystrosaurus* Zone fauna and the marine Sticky Keep fauna, sharing rhytidosteids and capitosaurids with both, a lydekkerinid only with the *Lystrosaurus* fauna and trematosaurids only with the Sticky Keep fauna.

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ABBREVIATIONS

c.m.	crista muscularis	pfr	prefrontal
cul.pr.	cultriform process	po	postorbital
ec	ectopterygoid	po.c.	postorbital canal/sulcus
ex	exoccipital	pp	postparietal
ext.n	external naris	pr.al	processus alaris
f	frontal	pr.b.	processus basalis
for.m.	foramen magnum	ps.ph	parasphenoid
int.v.	interpterygoid vacuity	pt	pterygoid
j	jugal	pt.f.	posttemporal fossa
jg.c.	jugal canal/sulcus	qd	quadrate
l	lacrimal	qd.pr.	quadrate process
lp.	stapedial lappet	qj	quadratojugal
mx	maxilla	qt	quadrate tubercle
n	nasal	sq	squamosal
ob.r.	oblique ridge	st	supratemporal
orb	orbit	sub.c.	suborbital canal/sulcus
ot.c.	otic canal/sulcus	sub.f.	subtemporal fossa
ot.n.	otic notch	supr.c.	supraorbital canal/sulcus
p	parietal	sup.sp.	supraoccipital space
pal	palatine	t	tabular
pal.pr.	palatine process	t.cr.ext.	crista tabularis externa
pf	postfrontal	X	foramen for vagal nerve
p.f.	parietal foramen		